



Modeling a version of the good-genes hypothesis: female choice of locally adapted males

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Abstract

In addition to other potential causes, immigration into locally adapted populations has been suggested to maintain the genetic variance in fitness that is necessary for the good-genes hypothesis. Using population-genetic simulations, the present contribution shows that co-occurring local adaptation and migration can maintain genetic variance in fitness. In combination with an effect of local adaptation on condition and condition-dependent sexual signaling, such a scenario therefore enables the evolution and maintenance of female choice for locally adapted males. The simulations show that this mechanism can also work when choice is costly, and that the potential benefit is similar to that in other good-genes mechanisms. As a consequence of female choice in favor of locally adapted males, differentiation between populations can be expected to increase due to the decreased effective gene flow between populations. Based on such effects, choice of locally adapted males has the potential to play an important role in speciation and adaptive radiation. © 2004 Elsevier GmbH. All rights reserved.

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Introduction

In many animal species, females do not mate at random but carefully choose among the available males and often prefer to mate with the most conspicuous ones. As a consequence of such directional sexual selection, males of many species have evolved extravagant morphological or behavioral traits (Andersson 1994). In contrast to the comparatively well-known effects of female choice, the causes of the evolution and maintenance of mate choice are less well understood (Andersson 1994). Theoretically, female choice can lead to direct benefits if the chosen males provide resources, protection or paternal care (see Arnqvist and Nilsson 2000). However, in many species males seem to provide nothing but sperm. In these cases any benefit of female choice has to accrue from the genetic quality of the

preferred mates. Historically, two dominant hypotheses for such indirect benefits of female choice have been distinguished. According to the good-genes hypothesis female choice leads to offspring of superior viability, whereas according to Fisher's sexual selection model female choice provides the benefit of an increased attractiveness of male offspring (see Andersson 1994 for a review of both hypotheses). Recently, Kokko et al. (2002) have shown that these two hypotheses are not alternatives but mere endpoints of a continuum. For the entire range, and thus also for either hypothesis, the evolution of female choice by indirect benefits depends on the existence of genetic variance in male fitness, because females can only benefit from choice if there are differences in the genetic quality of males. Any hypothesis for the evolution of female choice by indirect benefits therefore requires a mechanism for the maintenance of genetic variation. This is especially crucial if females are proposed to gain good genes, because

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natural and sexual selection for increased viability should deplete genetic variance in fitness (Fisher 1930). Two processes — deleterious mutations and co-evolutionary host–parasite cycles — have mainly been proposed to counteract this depletion of genetic variation and thus allow genetic variance in fitness to be maintained (Hamilton and Zuk 1982; Iwasa et al. 1991; Rowe and Houle 1996; Proulx 2001). Here, I will concentrate on another potential mechanism for the maintenance of genetic variance in male fitness: migration between locally adapted populations.

The basis of the argument is that if migration occurs between populations that differ in the conditions they are locally adapted to, individuals will appear in environments to which they are not adapted. Migration can therefore be expected to contribute to the maintenance of genetic variance because it causes genes to occur in environments where they decrease fitness (Phillips 1996; Storfer et al. 1999). There is plenty of evidence showing that local adaptation is widespread in plants and animals (e.g. Malhotra and Thorpe 1991; Nagy 1997; Karan et al. 1998; Van Zandt and Mopper 1998; Riechert and Hall 2000; for a review see Foster 1999), and differential local adaptation has also been observed in artificial selection experiments (Shirley and Sibily 1999).

More specifically, an important precondition of the hypothesis presented here has been shown in some of these studies: local adaptation had a large effect on male mating success (Dodd 1989; Ehrman et al. 1991; but see Hosken et al. 2002). Theoretically, the combined existence of local adaptation and migration between populations can thus maintain genetic variance in fitness as required for the good-genes hypothesis. Several authors have already noted that females should benefit from choosing locally adapted males under such circumstances (Taylor and Williams 1982; Charlesworth 1987; Iwasa et al. 1991). However, a specific theoretical treatment of such a scenario has been provided only recently: Proulx (2001) used an adaptive-dynamics approach and concluded from his complex analytical model that female choice of locally adapted males can evolve and that the highest level of female choice can be expected for intermediate levels of genetic heterogeneity within populations.

Here, I examine with relatively simple population-genetic simulations whether choice of locally adapted males can be adaptive. I also examine the potential cost of female choice for locally adapted males, that would still allow the evolution and maintenance of such female choice. For the simulations I assume condition-dependent courtship, i.e. that male courtship signals reveal male condition and that condition itself is influenced by local adaptation (as in Proulx 2001). Therefore, locally adapted males are able to produce signals of superior attractiveness because they are able to invest more in

signaling than males less adapted to the local conditions. This assumption of a connection between local adaptation and male mating success rests on an influence of the environment on the attractiveness of the males. This proposed influence is supported by empirical studies, which have shown that environmental conditions during ontogeny can influence the quality of courtship signals in various insects and birds (Markow and Toolson 1990; Olvido and Mousseau 1995; De Kogel and Prijs 1996; Droney 1996; Clark et al. 1997; Hoikkala and Isoherranen 1997; Griffith et al. 1999; Wagner and Hoback 1999). In addition, resident females often seem to prefer native males over immigrants (Verhulst and van Eck 1996; Bensch et al. 1998; MacDougall-Shackleton et al. 2002). Probably, the best evidence for mate choice with respect to local adaptation comes from a recent study on diet-dependent mate choice in a predatory mite (Lesna and Sabelis 1999). However, competition between males was not excluded in this study, and intrasexual selection might thus also have caused the mating advantage of locally adapted males.

There is also evidence that female fish prefer males of their own population over males of different origin (Luyten and Liley 1991; Ptacek and Travis 1997; Vamossi and Schluter 1999). Similar evidence for choice of local mates has also been found in a hermaphroditic snail (Rupp and Woolhouse 1999). However, all these studies on mate choice and local adaptations did not focus on examining the effect of local adaptation on attractiveness, so that the observed differences in attractiveness also might have been due to other causes. More importantly, male traits and female preferences might differ between populations in many of these cases (e.g. Houde and Endler 1990), so that female choice of local mates might be related to spatial divergence in sexually selected traits rather than to local adaptation. Clear evidence in favor of a role of local adaptation in the evolution of female choice is lacking, but this is probably due only to a lack of focused experiments. The aim of the model presented here is to show that theoretically the proposed mechanism can work, as well as to provide estimates for the selective advantage of a choice of locally adapted males and the likely consequences of such choice. As a next step, experimental studies are necessary to determine whether the proposed mechanism contributes to the evolution and maintenance of female choice and whether it has an influence on adaptive radiation, the fast evolution of ecologically diverging species.

Material and methods

I assumed two infinite populations of a diploid sexual animal with discrete generations and symmetrical

migration between populations. Migration rate m ($0 < m < 0.5$), the proportion of animals of both sexes that were assumed to migrate each generation from one to the other population, was varied to examine its influence on the potential advantage of mate choice. In my model, the migration rate is not allowed to evolve. It should be noted that migration might otherwise disappear, since local adaptation selects against migration between populations. This probably is not crucial for field conditions, because migration is likely to be beneficial itself or be maintained as an unavoidable pleiotropic consequence of some other beneficial aspect of life history (Morgan 2002; Saccheri and Brakefield 2002).

In the model, a single locus with two alleles was assumed to influence local adaptation such that the first allele was favored in population one and the second allele in population two. These alleles were assumed to be co-dominant and to influence juvenile survival. Individuals homozygous for the locally adapted allele were accordingly assigned a relative survival rate of 1, heterozygote individuals a rate of $1 - 0.5s$ ($0 < s < 1$), and homozygotes for the other allele were assigned a relative survival rate of $1 - s$; individuals maladapted to the present conditions thus were assumed to have a survival disadvantage of s . A second locus unlinked to the one responsible for local adaptation was assumed to influence female choice. A rare female-choice allele (usually I used a frequency of 0.01%) was introduced into populations consisting of randomly mating females. Females with the choice allele were assumed to prefer males that are homozygous for the locally adapted allele. For simplicity, I assumed that these females only mate with males adapted to the local conditions. Assuming a less stringent mechanism of choice would decrease the speed of evolution as well as any effects of choice. However, as long as choosy females mate much more often with locally adapted males, the effect of less stringent choice on the evolutionary outcome should be small. Compared to the preferred males, the males with one or two alleles coding for local adaptation in the other population were assumed to be in poorer condition resulting in less attractive advertisement signals. Choosy females were thus assumed to prefer locally adapted males due to their superior condition. The present model thus clearly is a special version of the good-genes hypothesis.

To examine whether in theory costly female choice can evolve, choosy females were assumed to show a reduction in fertility. As an effect of a cost of female choice of c ($0 \leq c \leq 1$), choosy females were assumed to have a relative fertility of $1 - c$ compared to the randomly mating females. In all these cases, the fate of the rare choice allele was determined to infer the theoretical conditions necessary for the evolution of female choice of locally adapted males. In the simula-

tions, the fate of the choice allele was examined under the assumption that the choice allele is either recessive or dominant compared to the random-mating allele.

The next series of simulations assumed that female choice of males can evolve with respect to a condition-dependent trait that provides information on the local adaptation of the males. In such a case, the presence of female choice of locally adapted males will have an influence on population heterogeneity and local adaptation because of directional selection for locally adapted males. To estimate the effect of such a process on population differentiation, I calculated the F_{ST} values for the modeled populations and compared the resulting values for random mating and choice of locally adapted males.

Results

Starting from an assumption that choice does not incur costs ($c = 0$), the frequency of the female choice allele increased to unity in all simulations whenever migration rate was assumed to be larger than zero. These simulations show that choice of locally adapted males is generally beneficial for females if immigration causes the maintenance of genetic variance in fitness. For costly female choice ($c > 0$), the disadvantage of immigrants, the immigration rate and the costs of choice determine whether a rare allele coding for a preference of locally adapted males can increase in frequency. However, the conditions for the evolution of female choice did not depend on dominance, and I received identical results for a recessive- and a dominant-choice allele. For immigration rates around a few percent per generation and a disadvantage of individuals less well adapted to the local conditions that is greater than about 10%, choice of locally adapted males is beneficial as long as costs of choice do not exceed a few percent. The maximum costs of choice that still allow the evolution of choice of locally adapted males are given in Fig. 1. The cost of choice that can be compensated by the benefits of choosing locally adapted males increases monotonically with the migration rate and with the advantage of local adaptation. In relation to these results, it should be noted that female choice could also evolve under high immigration rates ($m > 0.1$) that limit the genetic differentiation of populations.

As long as the costs of female choice did not exceed a threshold determined by the migration rate and the strength of local selection, i.e. the disadvantage of individuals maladapted to the local conditions, the allele coding for female choice increased in frequency. This increase in turn has an influence on the genetics of local adaptation. Since choosy females were assumed to prefer locally adapted males, males carrying the allele

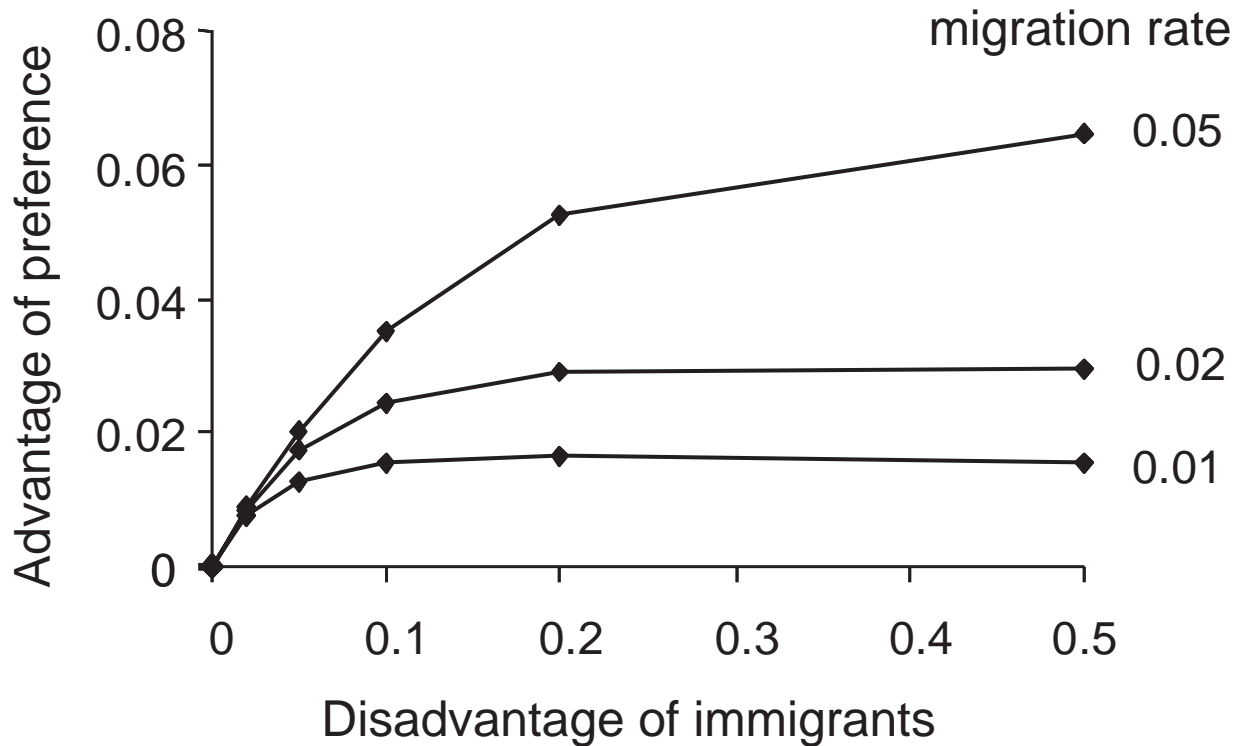


Fig. 1. Potential benefit of female choice as an effect of the disadvantage of immigrants (s ; equivalent to the benefit of locally adapted individuals) and of the migration rate m . The ordinate values of each point indicate the maximum cost of choice (c) that can be compensated by the benefits of female choice of locally adapted males. Whenever the cost of choice is lower than this value, female choice can evolve.

that leads to a decreased local adaptation have a reduced mating success. As a consequence, the extent of local adaptation and genetic differentiation between populations increases. To estimate the effect this process can have on population differentiation, I calculated the F_{ST} values for the two alleles coding for local adaptation under the assumption that all females prefer locally adapted males and under varying values of s and m . Compared with the F_{ST} values resulting when females mate at random, female choice of locally adapted males leads to a large increase especially for small values of s (Fig. 2). A female preference for locally adapted males can therefore cause increased population differentiation, and additional results show that this process is still possible at a relatively high migration rate.

Discussion

My simulations show that costly female choice of locally adapted males can evolve when migration leads to the maintenance of genetic variance in fitness. With a few percent increase in offspring fitness, the potential benefit of such choice is in the same range as had been estimated for the other suggested causes for the maintenance of genetic variance in the face of combined

natural and sexual selection, i.e. mutations and host–parasite co-evolutionary cycles (Heisler 1984; Kondrashov 1988; Kirkpatrick 1996; Kirkpatrick and Barton 1997). Likewise, the potential advantage of choosing males without selfish genes or without a resistance against selfish genes can be expected to be in a similar range in a system polymorphic for both meiotic drive and resistance (Reinhold et al. 1999). Thus, local adaptation theoretically seems to be as likely to be responsible for the maintenance of genetic variance in fitness as the other hypotheses (see also Proulx 2001). The empirical studies examining the indirect benefits of mate choice have returned similar ranges for the advantage of females choosing attractive males (Møller and Alatalo 1999). Local adaptation might also have an effect on sexual selection under Fisher's runaway sexual selection hypothesis. With a model similar to the one presented here, Day (2000) examined the effect of spatial variation in female preference and male traits on the evolutionary stable mating advantage due to Fisher's runaway process. He found that spatial variation can increase the likelihood for the maintenance of costly female choice when selective females benefit from producing attractive sons.

An interaction between local adaptation and sexual selection will have an influence on population genetics. If females prefer locally adapted males, this decreases

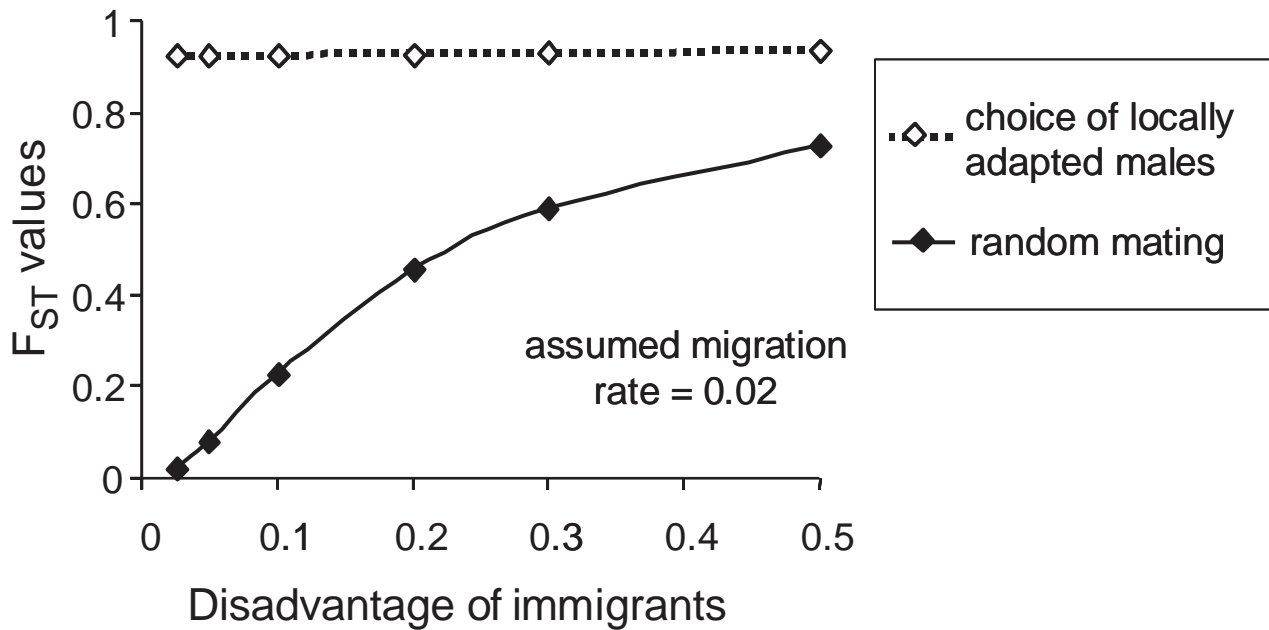


Fig. 2. Comparison of the effects of varying strength of local selection on population differentiation (measured as F_{ST} values with respect to locally selected alleles) between assumed random mating and female choice of locally adapted males. Migration rate $m = 0.02$.

the effective gene flow between populations which differ in their local adaptations. A similar effect, but in the opposite direction, occurs when offspring of immigrants show heterosis, leading to an increased gene flow (Ingvarsson and Whitlock 2000). As a result of the reduced gene flow caused by females choosing locally adapted males, the evolution of additional differences between populations is facilitated, and choice of locally adapted males may ultimately enhance the possibility of speciation (Proulx 2001). In line with this argument, sexual selection and spatial variation in environmental conditions were suggested to favor evolutionary branching and thus speciation in a recent theoretical study (Doebeli and Dieckmann 2003). Other population-genetic effects of a mating advantage of locally adapted males are proposed to include the facilitation of invasion into new niches and an increase in niche breadth (Proulx 1999). Different theoretical approaches thus suggest that an interaction of sexual selection and local adaptation has the potential to cause adaptive radiation, the evolution of genetically separated and ecologically diverged entities (species) within a relatively short period of time.

There is evidence that females prefer residents against immigrants in several animal species. In some fish and a snail, females prefer to mate with males of their own population when given a choice between males of different populations (Luyten and Liley 1991; Ptacek and Travis 1997; Rupp and Woolhouse 1999; Vamosi and Schluter 1999). Since the individuals used in these choice experiments were reared under identical condi-

tions in the laboratory, the observed assortative mating cannot be caused by a preference for locally adapted mates. However, these results are nevertheless consistent with the here-proposed preference for locally adapted mates. If such a type of choice has reduced the effective gene flow between populations, female preference can be expected to diverge among them, for instance when different signal traits confer information on local adaptation in different populations. However, one should note that the observed difference in female preference between populations and the resulting preference of females for males from their own population may also have diverged for other reasons. Female preference may, e.g. have diverged by drift in allopatry, or may have been influenced by ecologically divergent selection on females to avoid predators or to locate males.

Further, and less indirect, information on a potential influence of local adaptation on sexual selection can also be inferred from field studies in birds. In great reed warblers and great tits, resident females also seem to prefer native males against immigrants (Verhulst and van Eck 1996; Bensch et al. 1998; MacDougall-Shackleton et al. 2002), even though male traits probably do not differ between the involved populations. Also consistent with a preference for resident males, pied flycatcher breeding pairs with low genetic similarity were found to have significantly more extra-pair young in their nests (Rätti et al. 1995). Since these analytical studies did not focus on examining the effect of local adaptation on attractiveness, the difference in

attractiveness between residents and migrants might also be explained, e.g. by an increased migration tendency of less fit individuals. Specifically aimed experimental studies like the one by Lesna and Sabelis (1999) are therefore necessary to examine the proposed hypothesis that choice of locally adapted males contributes to maintain costly female choice.

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